

Cypraeidae: How well-inventoried is the best-known seashell family? *

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Abstract: Cowries (Cypraeidae) are diverse and occur in all tropical and some temperate seas, from shallow waters to the deep sea. There is a vast literature documenting the distribution, taxonomy, and shell variation, among many other topics. Because of its popularity among shell collectors, amateurs have contributed more to the cowrie literature than to most molluscan families. Traditionally, taxa have been described based on shell characters, and the majority of species descriptions continue to be published in non-peer-reviewed journals, magazines and books. Molecular studies in the last two decades have largely confirmed phylogenies based on morphology and anatomy. Currently, 245 species and 166 subspecies (or 411 operational taxonomic units) are recognized in 48 genera in the family. Despite being the best-known seashell family, the discovery curve suggests that there are still more taxa to be discovered. A review of the knowledge of the family is presented, and information on each genus is summarized.

Key words: morphological and molecular characters, inventory, species discovery curve, WoRMS, synonyms

Cowries (Caenogastropoda: Cypraeidae) are arguably the best-known seashells (Taylor 1979). Their polished and often colorful shells have attracted the attention of humans for thousands of years, and have been used for decoration, as currency, and in religious rituals. Cowries are very popular among shell collectors and most shell collections have at least some cowries; Dance (1966) suggested that shell collecting started with cowries. They are found worldwide; most species live in shallow and warm waters and share similar distribution with hard corals (Taylor 1979), but a few species live in temperate waters.

The goal of this paper is to review the literature, summarize the knowledge on cowrie diversity, and document the progress of its inventory.

The Cypraeidae have a rich literature spanning from scientific to popular, covering a wide gamut of topics. There are perhaps more monographs and books dedicated to the Cypraeidae than to any other molluscan family (e.g., Gray 1824, Jousseaume 1884, Roberts 1885, Melvill 1888, Hidalgo 1906–1907, Schilder and Schilder 1938–1939, 1971, Allan 1956, Burgess 1970, 1985, Walls 1979, Liltved 1989, Lorenz and Hubert 1993, 2000, Lorenz 2001, 2002, Wilson and Clarkson 2004); there is even a book dedicated to a single species: a study of the Hawaiian endemic *Cribrarula gaskoini* (Reeve, 1846) (Dayle and Heiman 2011).

Several iconographies illustrate well the diversity in the family (e.g., Sowerby 1870, Burgess 1970, 1985, Walls 1979, Lorenz and Hubert 1993, 2000, Poppe 2008); some also illustrate live animals (e.g., Johnson 2008–2013). Most books on seashells from tropical regions include cowries. Several works focus on regional faunas (e.g., Hawaii: Schilder 1933, Ingram 1937, 1947, Kay 1961, Cate 1965; Australia: Iredale 1935, 1939, Lorenz 2001, Darrah 2002, Wilson and Clarkson 2004; New Caledonia: Dautzenberg 1952, Chatenay 1977; Fiji: Cernohorsky 1964; Philippines: Cate 1966; Okinawa: Cate 1967; Mauritius: Schilder 1960a, Boizot *et al.* 1985; South Africa: Liltved 1989; Red Sea: Heiman 2000). *The Cowry* was a small journal dedicated to cowries published between 1960–1965 (R. J. Griffiths, ed.). A colorful new magazine, *Beautifulcowries*, has recently been launched as a new outlet solely for cowrie articles (Passamonti 2012).

Among the topics discussed in cowrie publications are: distribution (e.g., Schilder and Schilder 1938–1939, Schilder 1965, 1969, Lorenz and Hubert 1993, 2000); geographic variation (e.g., Schilder and Schilder 1938–1939, Irie 2006); and species complexes (e.g., Lorenz 2001, 2009, Moretzsohn 2003, Lorenz and Chiapponi 2005). Many articles concern the description of new taxa (e.g., Burgess 1993, Lorenz 2002, Moretzsohn 2002a, 2007); taxonomic revisions of genera or species complexes are less common

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(e.g., Darragh 2002, Lorenz and Chiapponi 2005). The classification of the Cypraeidae has been a topic of discussion (e.g., Schilder and Schilder 1938–1939, 1971, Schilder 1941, Steadman and Cotton 1946, Kay 1957, 1960a, Meyer 2003, 2004). In response to increasing splitting of genera, which reached 61 (Steadman and Cotton 1946), Kay (1957) proposed classifying all cowries in the single genus *Cypraea* Linnaeus, 1758. Several authors followed her advice (e.g., Burgess 1970, 1985, Walls 1979, Liltved 1989), while others called groups of species either species complexes, subgenera or genera (e.g., Schilder and Schilder 1971, Lorenz and Hubert 1993, Meyer 2003, 2004). Shell collectors tend to prefer the simplicity of a single genus, but scientists and more specialized collectors use a classification based on phylogenetic relationships.

Traditionally, cowrie classification has been based primarily on shell characters, despite the plasticity of such characters and the lack of shell sculpture and a visible protoconch in the adult shell. A few authors have used anatomical characters (e.g., mantle: Burgess 1983; radula: Bradner and Kay 1995, 1996, Lorenz 1998, Moretzsohn 2002a, 2002b, 2004), or sought novel taxonomic characters (e.g., protoconch: Ranson 1967, Foin 1982; odontophores, shell spotting, and dorsal line angle: Moretzsohn 2002b, 2003). Molecular characters have been used in the past two decades with the advent of molecular systematics and improvements in DNA sequencing technology; the effort was championed by Meyer (2003, 2004, 2005).

In contrast, studies of the animal (other than the shell) have received less attention, but there are some good studies on: biology and life history (e.g., Taylor 1979, Kay 1985, Katoh 1989, Wilson 1998, Wilson and Clarkson 2004); ecology (e.g., Hayes 1983, Lorenz 1998, 2000); anatomy (e.g., Schilder 1936, Kay 1957, 1960b, Gosliner and Liltved 1985, Simone 2004); mantle (e.g., Thompson 1961, Burgess 1983, Kay 1985); sperm (Healy 1986); reproduction (Ostergaard 1950, Taylor 1975, Wilson 1985, Osório *et al.* 1999, Meyer 2003, Wilson and Clarkson 2005); behavior (e.g., Ostergaard 1950, Renaud 1976), etc. Other topics that appear less frequently include evolution (e.g., Kay 1996, Meyer 2003, 2004, 2005), phylogeny (e.g., Schilder 1936, 1939, Ranson 1967, Meyer 2003, 2004, Lopez Soriano 2006), and fossils (Beddome 1898, Schilder 1932, 1935, Kay 1990, Darragh 2002, Groves 2010).

Intraspecific variation has been discussed at length (shell morphometrics: e.g., Schilder and Schilder 1934, 1952, Orr 1959, Schilder 1960b, Tissot 1984, Moretzsohn 2002a, Heiman 2004, 2005, Dayle and Heiman 2011). Sexual dimorphism in shell size has been documented in several species (e.g., Orr 1959, Griffiths 1961, Schilder and Schilder 1961, Moretzsohn 2002a, Irie and Adams 2007, Irie and Morimoto 2008). Among the species studied, females usually tend to have a larger shell than males, but in a few species the opposite is true (Schilder and Schilder 1962). Sexual dimorphism has also

been reported in the radula and odontophores (*Cribrarula gaskoini*: Moretzsohn 2003); more studies are needed to verify if the same also occurs in other species that show dimorphism in shell size.

There are six major biogeographical regions where cowries are found (“cowrie provinces”): 1) Indo-Pacific; 2) southern Australian; 3) South African; 4) Mediterranean and West African; 5) Caribbean; and 6) West American. The Indo-Pacific is by far the largest and richest province, and includes the most widely-distributed species, as well as many with restricted ranges. The majority of cowries possess planktonic veliger larvae that can have long larval duration and good dispersal ability, which accounts for some widely-distributed species in the Indo-Pacific. In contrast, in a few regions with upwelling and/or high latitude, direct development has evolved independently at least five times (Meyer 2003). The following genera have crawl-away juveniles: *Cypraeovula* Gray, 1824 in southern Africa, *Barycypraea* Schilder, 1927 in southern Africa and Oman; *Austrocypraea* Cossmann, 1903, *Notocypraea* Schilder, 1927, *Umbilia* Jousseaume, 1884, and *Zoila* Jousseaume, 1884 in southern Australia; and *Muracypraea* Woodring, 1957 in northern Colombia and Venezuela. The latter genus occurs in low latitude but in upwelling areas (Meyer 2003).

MATERIALS AND METHODS

The list of valid species and subspecies used in this analysis was downloaded from the WoRMS database (WoRMS Editorial Board 2013) on 24 February 2013. Although WoRMS was created in 2008 as an outgrowth of the European Register of Marine Species, some entries in the Cypraeidae date back to at least 1997. I became the first taxonomic editor of the Cypraeidae in December 2010. Since then, I have attempted to clean up, complete the listing of all valid taxa, and add sources (citations), but to date little effort has been made to enter synonyms.

The distribution of cowries is well known and populations are reasonably well documented, therefore, subspecies are commonly recognized in the cowrie literature. Additionally, there are many more named taxa such as varieties and forms that are used by shell dealers and the shelling community, but those names are not governed by the International Code of Zoological Nomenclature; generally infrasubspecific taxa are not included in WoRMS and, therefore, not included in this analysis.

The distribution range maps (Fig. 1) of 209 Indo-Pacific species were traced into ArcGIS 8.3 based primarily on Burgess (1985), Lorenz and Hubert (2000), and Lorenz (2002), and complemented with vetted museum records. Figure 1 was modified from a work on Indo-Pacific biodiversity (Moretzsohn and McShane 2004); hence only species from that region were included (with a few extralimital cowries).

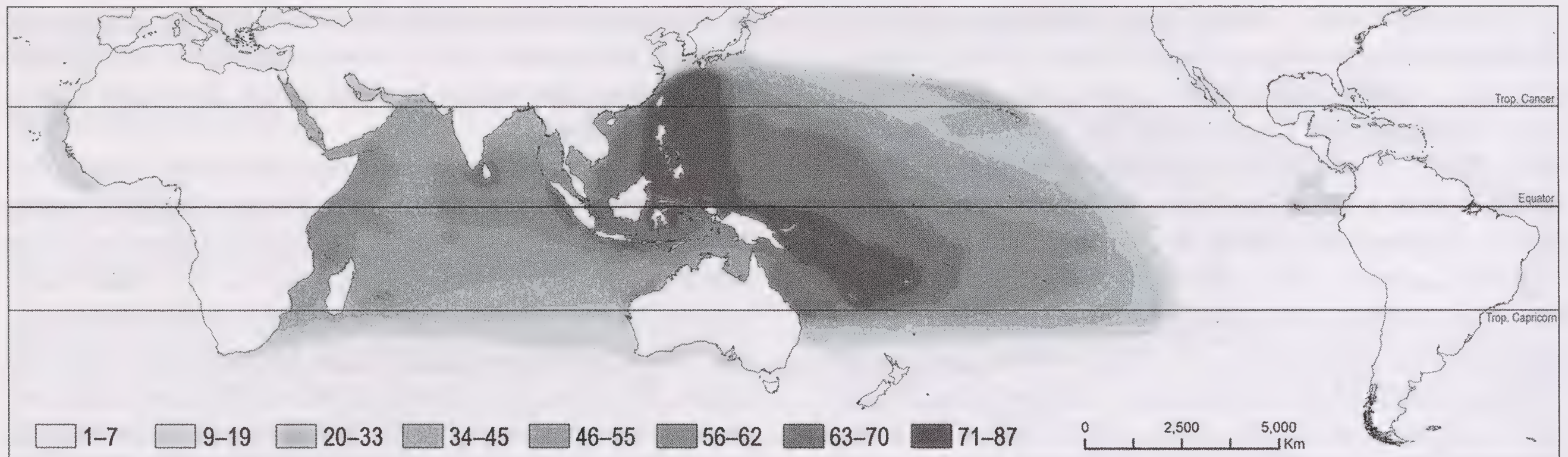


Figure 1. Pattern of diversity based on the distribution of 209 Indo-Pacific cowries. Figures represent species richness (modified from Moretzsohn and McShane 2004). (Color shown in electronic version only).

The Cypraeidae taxon list was downloaded from WoRMS in MS Excel format. Then, the following criteria for operational taxonomic units (OTU) (modified from Meyer 2004) were applied: 1) geographic distinction or allopatry; 2) taxonomic recognition by previous workers; and, 3) significant genetic distance or anatomical difference from sister group. An OTU was included in analyses only if at least two of the above criteria were met; alternate representation taxa, and fossil species were removed from the analysis.

Histograms of number of taxon descriptions were calculated using the online Free Statistical Software (Wessa 2012) and imported into MS Excel; pie charts and species discovery curves were produced in MS Excel 2010. Shell length and bathymetric ranges were obtained mainly from Burgess (1985), Lorenz and Hubert (1993), and Lorenz (2002), in addition to other sources; OTUs with incomplete shell size or depth data were excluded. Modal sizes and depths were determined from a database containing all available data compiled for all OTUs.

Authors' country of origin were obtained mainly from Coan *et al.* 2012, and several other sources; individual co-authors were accounted for in the pie charts of authors and countries (Fig. 3A, B), hence the number of entries is larger than the number of taxa. Note that although Franz A. Schilder was born in Austria, he grew up and worked in Germany and is often referred to as German, thus he was coded here as German.

For Appendix 1, authorities of genera and type species were found in Schilder and Schilder (1971), Lorenz and Hubert (2000), and Meyer (2003). The number of OTUs per genus was obtained from WoRMS (Moretzsohn and Gofas 2013). Shell size range, bathymetric range and distribution represent the extremes for each entire genus. Information on direct developers was found in Meyer (2003).

RESULTS

As of 24 February 2013 there were a total of 245 species and 166 subspecies recognized as valid in the Cypraeidae (Moretzsohn and Gofas 2013), or 411 OTUs (Appendix 1). The number of genera currently accepted is 48, with an average of 8.6 OTUs per genus. Seven genera are monotypic, and ten genera have 15 or more OTUs.

Most cowries are found in the tropics but a few species live in temperate waters in latitudes as high as 44°N (Savona, Italy) and about 42°S (Tasmania, Australia) (Beddome 1898). There is a latitudinal gradient in species diversity, with species richness increasing toward the tropics (Fig. 1), where cowries often share similar distribution with hard corals and live in shallow waters (Taylor 1979). The highest diversity of cowries is found in the Indo-West Pacific (IWP), in the region known as Coral Triangle, an area encompassing most of Indonesia, Malaysia, the Philippines, Papua New Guinea, the Solomon Islands, East Timor, and Brunei, with 71 to 87 species observed (out of 209). The region extending to Vanuatu, Fiji, and New Caledonia is also very diverse (Moretzsohn and McShane 2004). The Central Pacific and Indian Ocean have many cowries in common with the IWP, although some species are restricted to either one or the other ocean basins. Some species, such as *Monetaria caputserpentis* (Linnaeus, 1758) have teleplanic larvae and are widely distributed throughout most of the Indo-Pacific. Hawaii is more isolated and has fewer cowries than the Central Pacific, but some OTUs are restricted to the archipelago.

Discovery and documentation

Between 1758–1771 Linnaeus described 39 species (and the first few synonyms, in addition to one species now in the family Triviidae). His species include the most widespread

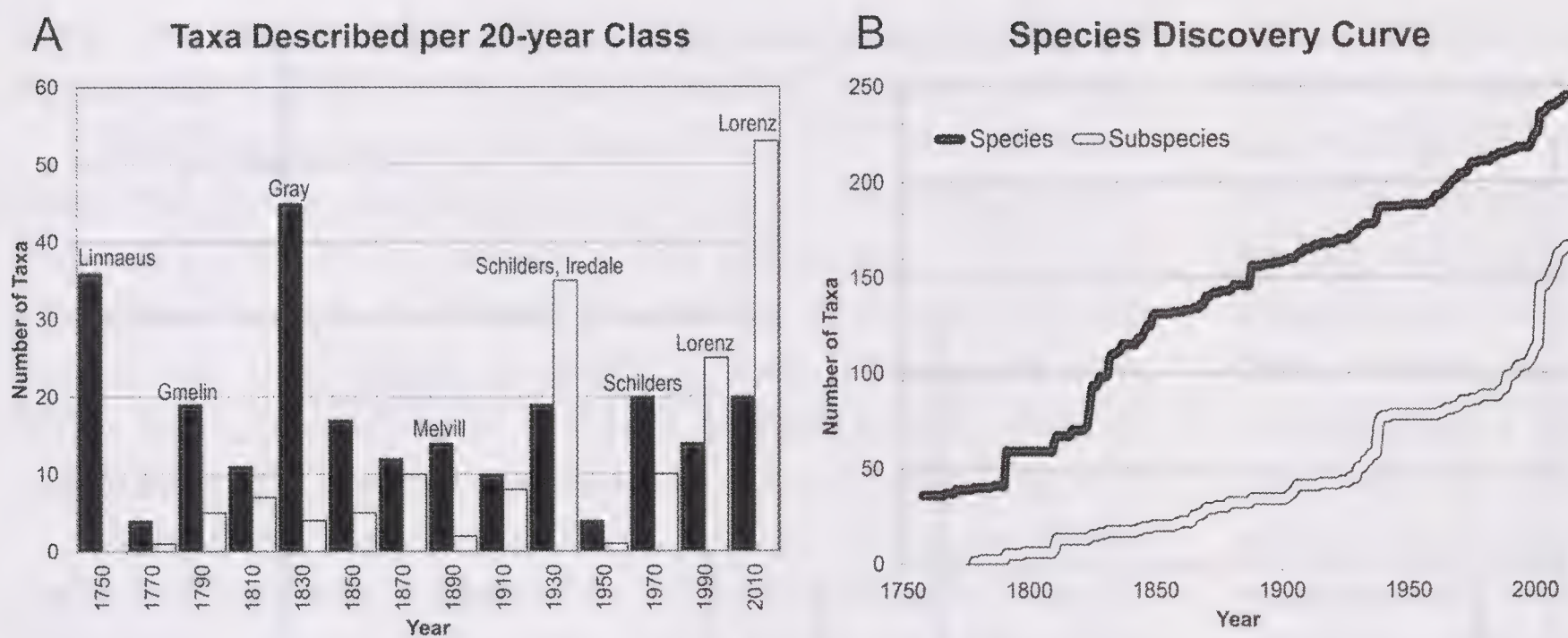


Figure 2. Species (black bars) and subspecies (white bars) descriptions in the Cypraeidae. **A**, Number of taxa described per 20-year class; some peaks are identified by the most prolific authors. **B**, Species discovery curve.

(*Monetaria caputserpentis*), the largest shell (*Macrocypraea cervus* (Linnaeus, 1771)), and some of the most common species in the family (e.g., *Monetaria moneta* (Linnaeus, 1758)).

With the advent of oceanic navigation and world commerce, collection of shells and other natural history specimens turned into fashionable items in Europe. The drive to provide novelties eventually led to the most productive era, known as the “Golden Age of Discoveries,” in the first half of the 19th Century, with John E. Gray being the most prolific author; the number of cowrie species more than tripled between 1800–1900. The rate of new species discovery remained steady since the mid-1800’s to present (Fig. 2A–B), but the descriptions of new subspecies increased substantially since then, with an early peak in the 1930’s thanks to the work of the Schilders and Tom Iredale. World War II took a toll also on new discoveries, but they resumed in the 1960’s, again led by the Schilders.

been said that only twice did they observe live cowries. That fact may have compromised their understanding of the importance of studying the living animal (Griffiths 1971).

Since the mid-1980’s and continuing to date, another German, Felix Lorenz, has led the descriptions of new cowries. Lorenz is a biologist and shell dealer with access to large quantities of specimens, many self-collected; he has authored over 100 papers and several books (e.g., Lorenz and Hubert 1993, 2000, Lorenz 2001, 2002) on cowries (and other mollusks). In the 21st Century, Lorenz has collaborated with molecular biologist Chris Meyer, by providing ample material for molecular studies (Meyer 2003, 2004), which uncovered a large cryptic diversity; many taxa were promptly described (e.g., Lorenz 2002).

An analysis of the authors (and co-authors) of cowrie OTUs showed that the top seven authors have described about half of all OTUs, with Lorenz having described more

OTUs than any other author, with 69 OTUs, followed F. A. Schilder (41), Linnaeus, Gray, Gmelin, M. Schilder, and Melvill (Fig. 3A). [The late Raybaudi Massilia, a shell dealer, named about 400 taxa, but most are invalid or synonyms (Groves and Weil 2002). The Schilders also named hundreds of taxa but most are infrasubspecific].

Additionally, although few cowries occur in the Mediterranean, the majority of taxa were described by Europeans (> 80%), and relatively few authors were from countries where cowries occur. Germany was the country that contributed the most OTUs (36%), thanks to the work of Gmelin, the Schilders, and Lorenz (Fig. 3B). About 93% of species were described by single authors, and

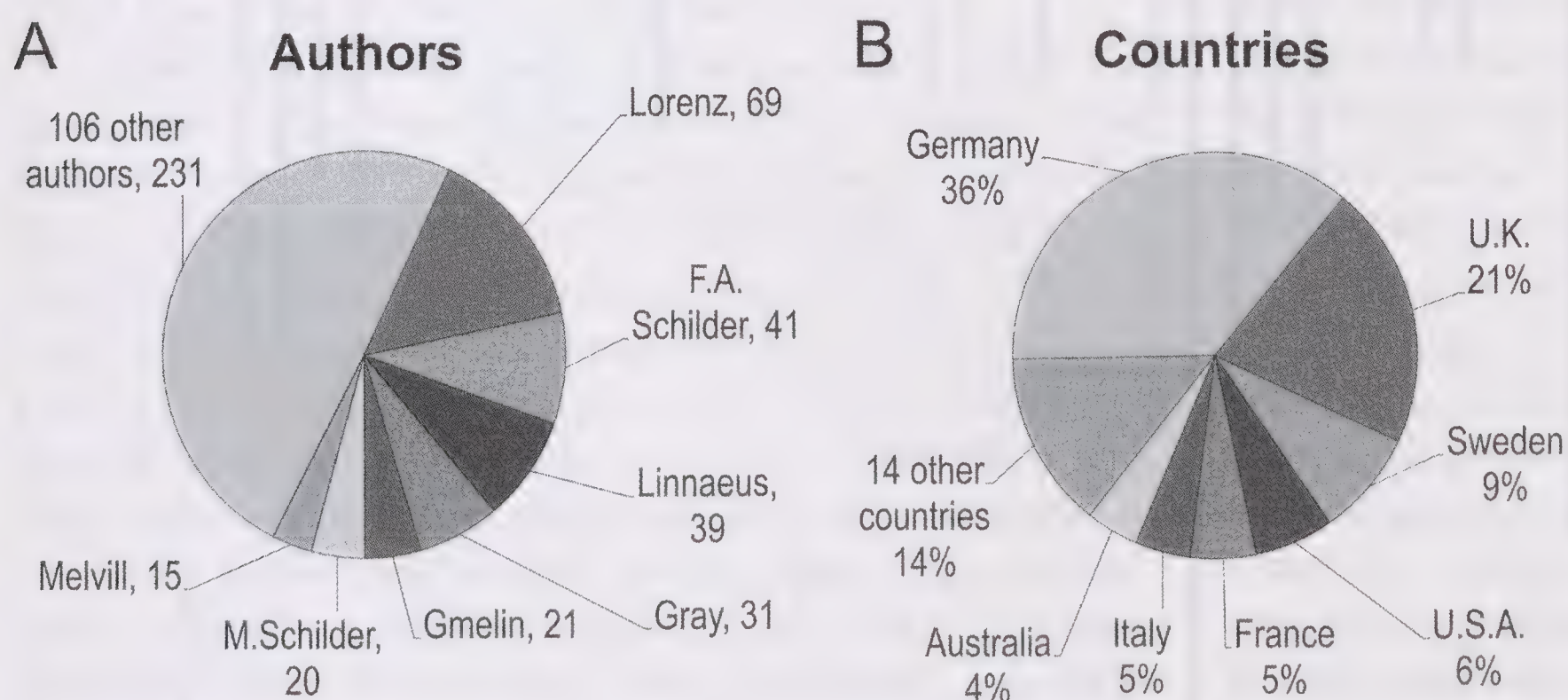


Figure 3. Authors and co-authors of OTUs in the Cypraeidae. **A**, The top seven most prolific authors and the number of OTUs they described that are considered valid. **B**, The top seven countries of origin of cowrie taxa authors; figures represent the percentage of taxa that were described by authors from each country.

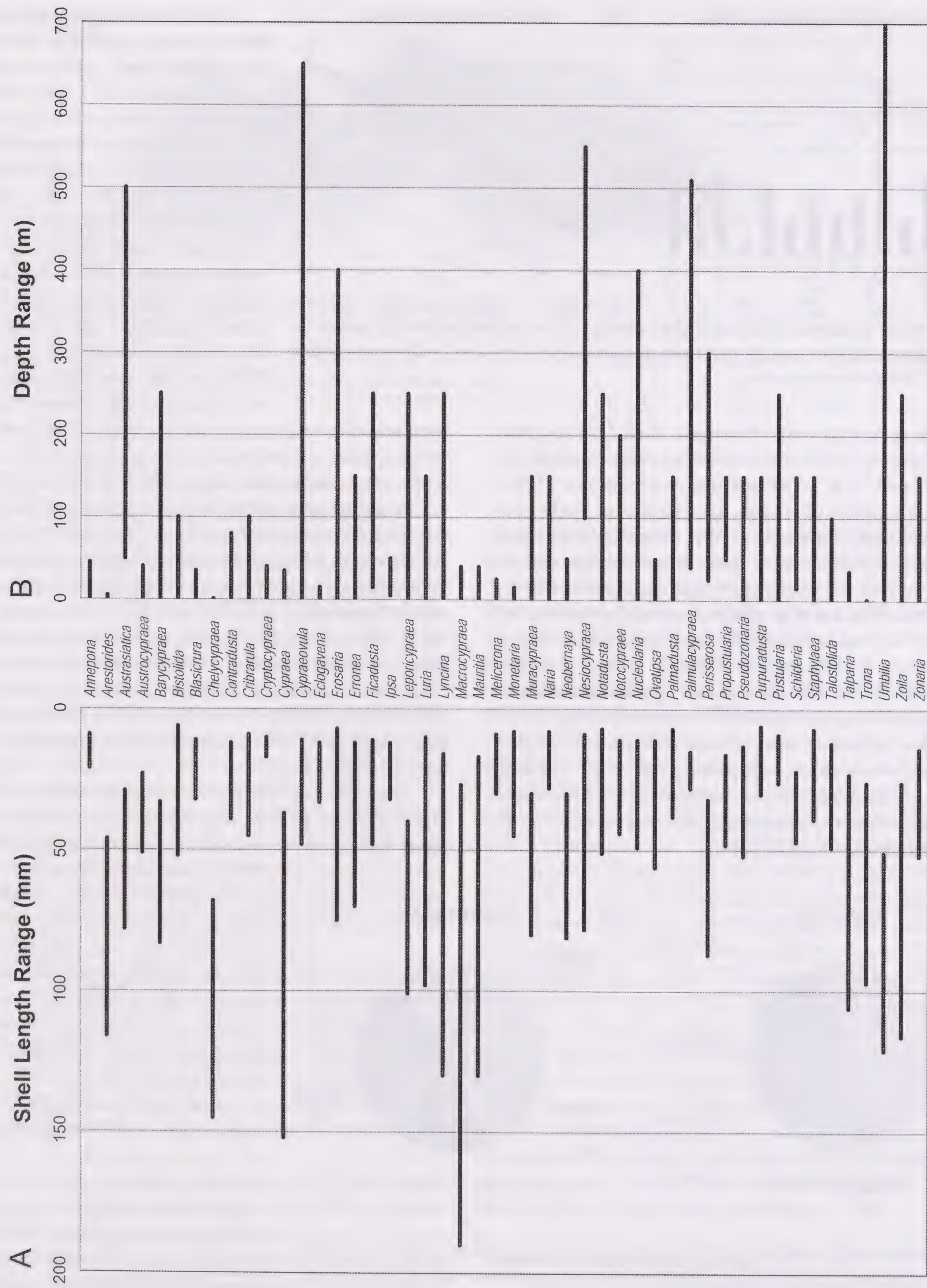


Figure 4. Ranges per genus. A, Shell length range (in mm) and, B, bathymetric range (in m).

7% by two authors, while 73% of subspecies were described by single authors, 25% by two authors, and 1% by three authors.

Shell length ranges were found for 317 OTUs, and from those, the modal shell length was about 25 mm long, with a range of 6–190 mm in the family. Five genera have OTUs with modal shell length of 15 mm or less; five genera have OTUs with modal shell length of about 70 mm. Ten genera have OTUs that can reach over 100 mm in shell length, while 22 genera have OTUs with a maximum length of 50 mm (Fig. 4A).

Bathymetric ranges were found for 282 OTUs; the modal depth was 5 m, with a range of 0–700 m in the family (Fig. 4B, Appendix 1). About 60% of the OTUs for which bathymetric range is known can be found in the intertidal zone or up to 2 m deep. Seven genera have species that reach 300 m or deeper (Fig. 4B). The deepest-living cowrie, *Umbilia capricornica* Lorenz, 1989, may reach a depth of 700 m (Lorenz and Hubert 2000).

DISCUSSION

Cowries are well known and their distributions have been well documented. Most cypraeid taxa have been described in non-peer review literature, based largely or solely on shell characters. Many new taxa are proposed with little scientific basis and upon closer scrutiny turn out to be synonyms of already known taxa, or represent anomalies in the normal range of intraspecific variation. Amateurs (defined as those not employed as practicing malacologists) have made important contributions to the cowrie studies such as describing new taxa, and providing material and information to malacologists. However, amateurs (and professionals) have also contributed a great deal of ‘noise’ to taxonomy with the introduction of unnecessary names. Taylor (1979) estimated that there were well over 1,000 names when less than 200 species were recognized, or over 5 synonyms per valid species in the Cypraeidae.

Besides the genuine desire to make scientific contributions, other motivations to describe new taxa include: 1) the vanity to have one’s name attached to a taxon (either as describer or as a patronymic), and 2) economic gain. The latter is a well-known phenomenon: collectors pay a premium for any ‘new’ taxon (at least until it is disregarded as a synonym). These problems are neither new nor restricted to the cowries; many ‘seashell’ families (*sensu* Bouchet *et al.* 2011), butterflies, and other collectible organisms are also plagued with synonyms.

Many species have medium to large shells (Fig. 4A), and most cowries live in shallow waters (Fig. 4B), where they tend to be conspicuous reef-dwellers (albeit nocturnal), therefore, it is expected that most cowries have already been discovered. However, contrary to expectation, new species discoveries have continued on a steady pace since the 1850’s to present. In contrast, subspecies descriptions were not common during the “Golden Age of Discoveries,” but have become increasingly

so from the 1930’s to present. As a result, despite being one of the best-documented groups of mollusks, cowrie discovery curves (Fig. 2B) suggest that there may be still more cowries to be discovered. With the increased popular interest in shells, widespread scuba diving, expeditions in search of new discoveries (*e.g.*, Bouchet 2009, Bouchet *et al.* 2011), and the recent advent of molecular systematics, we are currently experiencing a “New Golden Age of Discoveries” (Fig. 2A), especially in non-‘seashell’ families (*e.g.*, Turridae, Pyramidellidae, Eulimidae, Galeommatidae, etc.), although description of new species is a challenge to taxonomists (Bouchet 2009). However, the cowrie discovery curves on Fig. 2B are likely to be inflated; once genera are reviewed, many recently-described taxa may turn out to be synonyms.

The new discoveries in cowries are expected to come from populations that: 1) hide in plain view as cryptic diversity and are likely to be discovered using molecular and/or detailed anatomical data; 2) live in deep water; 3) have limited distribution; and, 4) occur at the edges of distribution of known taxa. Included among the candidates with possible cryptic diversity are the seven genera with direct development, in particular *Cypraeovula* and *Zoila*, where large numbers of subspecies have been recognized (at least on a conchological basis) in populations with limited ranges. Further scrutiny, including anatomical and molecular data, is necessary to confirm the discoveries.

Meyer (2003, 2004) produced molecular phylogenies based on nearly comprehensive sampling of cowries from most known OTUs, only missing the more elusive OTUs. Overall, he found remarkable congruence with OTUs recognized by morphological characters and allopatry. Most of the so-called species complexes, genera or subgenera were found to be monophyletic with strong support. Meyer (2004) compared his results with the most recent checklist of the cowries at the time (Lorenz 2002) and about 93% of the species recognized by Lorenz were also Evolutionary Significant Units (ESU), and about 70% of the subspecies listed in Lorenz (2002) were recognized by molecular characters as ESU. In addition, 20 ESU showed cryptic diversity and had not been described by then (although most of them have been described by Lorenz since then).

The highest diversity of Cypraeidae occurs within the Coral Triangle (Fig. 1), the epicenter of marine biodiversity. The cowrie biodiversity gradient has a bull’s eye pattern, with decreasing species richness as one moves away from the Coral Triangle, a pattern congruent with results from a study of over 10,000 marine species (about 80% of which reef fishes, but also mollusks, corals, crustaceans, seagrasses and mangroves) (Sanciangco *et al.* 2013). The Philippines and adjacent areas, with a complex patchwork of shallow and deep water habitats, are particularly rich in cowries. It is not surprising that most of the cowries (and seashells in general) in the shell collectors market come from the Philippines.

There are concerns about overexploitation of marine resources in the Philippines and elsewhere, especially because of the damaging effects of trawling (more for fish resources rather than shells). Most cowries occur within scuba and hookah diving range (Fig. 4B) and are collected manually by waders and divers, therefore, the damage to the habitat from the collection of shells is much lower than commercial fisheries or pollution. However, because cowries are valuable as specimen shells, especially the rare species, there is a great pressure where they occur in large numbers, and exploitation may be reaching unsustainable levels. More detailed studies are needed to assess the impact of commercial shell collecting on natural resources, and the conservation status of cowries.

Other topics that still remain largely unknown or which deserve further attention in cowries include: generic revisions and better characterization of genera on a morphological basis; ecology and study of live animals in the field to document behavior (e.g., parental care of eggs) and life history; comparative anatomical studies; function of the mantle and its papillae; function of shell color and its secretion pathways (also the factors that influence “albinism”, “melanism” and rostration); sexual dimorphism; cryptic species; hybridization; speciation and phylogeny, among others.

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Appendix 1. Genera of the Cypraeidae with the type species, number of operational taxonomic units (OTUs), shell length range (mm), bathymetric range (m), and geographic distribution of each genus. Genera marked with an asterisk represent direct developers (Meyer 2003).

Genus	Type species	No. OTUs	Shell length range (mm)	Depth range (m)	Distribution
<i>Annepona</i> Iredale, 1935	<i>Cypraea annulata</i> Gray, 1828 (= <i>mariae</i> Schilder, 1927)	1	9–21	0–45	Pacific, East Africa
<i>Arestorides</i> Iredale, 1930	<i>Cypraea argus</i> Linnaeus, 1758	3	46–116	0–5	Indo-Pacific
<i>Austrasiatica</i> Lorenz, 1989	<i>Schilderia sakuraii</i> Habe, 1970	7	29–78	50–500	Pacific
* <i>Austrocypraea</i> Cossmann, 1903	<i>Cypraea contusa</i> McCoy, 1877 (Late Miocene)	1	23–51	0–40	NW to S Australia
* <i>Barycypraea</i> Schilder, 1927	<i>Cypraea (Aricia) caputviperae</i> Martin, 1899 (Late Miocene)	4	33–83	0–250	Arabian Sea to South Africa
<i>Bistolida</i> Cossmann, 1920	<i>Cypraea stolidia</i> Linnaeus, 1758	25	6–52	0–100	Indo-Pacific
<i>Blasicrura</i> Iredale, 1930	<i>Cypraea pallidula rhinoceros</i> Souverbie, 1865	5	11–32	0–35	Indian Ocean to Central Pacific
<i>Chelycypraea</i> Schilder, 1927	<i>Cypraea testudinaria</i> Linnaeus, 1758	1	68–145	0–1	Indo-Pacific
<i>Contradusta</i> Meyer, 2003	<i>Cypraea walkeri</i> Sowerby I, 1832	2	12–39	0–80	Indian Ocean to Central Pacific
<i>Cribrarula</i> Strand, 1929	<i>Cypraea cribraria</i> Linnaeus, 1758	25	9–45	0–100	Indo-Pacific
<i>Cryptocypraea</i> Meyer, 2003	<i>Cypraea dillwyni</i> Schilder, 1922	1	10–17	0–40	Central Pacific
<i>Cypraea</i> Linnaeus, 1758	<i>Cypraea tigris</i> Linnaeus, 1758	3	37–152	0–35	Red Sea, Indo-Pacific
* <i>Cypraeovula</i> J. E. Gray, 1824	<i>Cypraea capensis</i> J. E. Gray, 1828	36	11–48	1–650	Southern Africa
<i>Eclogavena</i> Iredale, 1930	<i>Cypraea coxeni</i> Cox, 1873	6	12–33	0–15	Western Pacific
<i>Erosaria</i> Troschel, 1863	<i>Cypraea erosa</i> Linnaeus, 1758	34	7–75	0–400	Red Sea, Indo-Pacific
<i>Erronea</i> Troschel, 1863	<i>Cypraea erronea</i> Linnaeus, 1758	28	12–70	0–150	Red Sea, Indo-Pacific
<i>Ficadusta</i> Habe and Kosuge, 1966	<i>Cypraea pulchella</i> Swainson, 1823	5	11–48	15–250	Indian Ocean to Western Pacific
<i>Ipsa</i> Jousseau, 1884	<i>Cypraea childreni</i> Gray, 1825	2	12–32	5–50	Indo-Pacific
<i>Leporicypraea</i> Iredale, 1930	<i>Cypraea mappa</i> Linnaeus, 1758	7	40–101	0–250	Indo-Pacific
<i>Luria</i> Jousseau, 1884	<i>Cypraea lurida</i> Linnaeus, 1758	9	10–98	0–150	Mediterranean, Indo-Pacific, Atlantic
<i>Lyncina</i> Troschel, 1861	<i>Cypraea lynx</i> Linnaeus, 1758	20	16–130	0–250	Red Sea, Indo-Pacific
<i>Macrocypraea</i> Schilder, 1930	<i>Cypraea exanthema</i> Linnaeus, 1767 (= <i>zebra</i> Linnaeus, 1758)	3	27–190	0–40	Eastern Pacific, Western Atlantic
<i>Mauritia</i> Troschel, 1863	<i>Cypraea mauritiana</i> Linnaeus, 1758	14	17–130	0–40	Indo-Pacific
<i>Melicerona</i> Iredale, 1930	<i>Cypraea listeri</i> Gray, 1824	3	9–30	0–25	Indian Ocean to Western Pacific
<i>Monetaria</i> Troschel, 1863	<i>Cypraea moneta</i> Linnaeus, 1758	6	8–45	0–15	Indo-Pacific
* <i>Muracypraea</i> Woodring, 1957	<i>Cypraea mus</i> Linnaeus, 1758	3	30–80	1–150	Venezuela and Colombia
<i>Naria</i> Gray, 1832	<i>Cypraea irrorata</i> (Gray, 1828)	2	7–24	1–150	Central Pacific
<i>Neobernaya</i> Schilder, 1927	<i>Cypraea spadicea</i> Swainson, 1823	1	30–81	0–50	California
<i>Nesiocypraea</i> Azuma and Kurohara, 1967	<i>Nesiocypraea midwayensis</i> Azuma and Kurohara, 1967	7	9–78	100–550	Eastern Africa to Western Pacific
<i>Notadusta</i> Schilder, 1935	<i>Cypraea victoriana</i> Schilder, 1935 (Late Miocene)	7	7–51	0–250	Eastern Africa to Central Pacific
* <i>Notocypraea</i> Schilder, 1927	<i>Cypraea piperita</i> Gray, 1824	7	11–44	0–200	Southern Australia
<i>Nucleolaria</i> Oyama, 1959	<i>Cypraea nucleus</i> Linnaeus, 1758	6	11–49	0–400	Indo-Pacific
<i>Ovatipsa</i> Iredale, 1931	<i>Cypraea chinensis</i> Gmelin, 1791	8	11–56	0–50	Indo-Pacific
<i>Palmadusta</i> Iredale, 1930	<i>Cypraea clandestina</i> Linnaeus, 1767	24	7–38	0–150	Red Sea, Indo-Pacific
<i>Palmulacypraea</i> Meyer, 2003	<i>Erronea (Gratiadusta) katsuae</i> Kuroda, 1960	5	15–28	40–510	West to Central Pacific
<i>Perisserosa</i> Iredale, 1930	<i>Cypraea guttata</i> Gmelin, 1791	2	32–87	25–300	Indian Ocean to West Pacific

Appendix 1. (Continued)

Genus	Type species	No. OTUs	Shell length range (mm)	Depth range (m)	Distribution
<i>Propustularia</i> Schilder, 1927	<i>Cypraea surinamensis</i> Perry, 1811	1	16–48	50–150	Florida to Brazil
<i>Pseudozonaria</i> Schilder, 1929	<i>Cypraea arabicula</i> Lamarck, 1810	5	13–52	0–150	Galapagos and Tropical Eastern Pacific
<i>Purpuradusta</i> Schilder, 1939	<i>Cypraea fimbriata</i> Gmelin, 1791	17	6–30	0–150	Indo-Pacific
<i>Pustularia</i> Swainson, 1840	<i>Cypraea cicercula</i> Linnaeus, 1758	15	9–26	0–250	Indo-Pacific
<i>Schilderia</i> Tomlin, 1930	<i>Cypraea utriculata</i> Lamarck, 1810 (Pliocene)	2	22–47	15–150	Mediterranean to Angola and Gulf of Biscay
<i>Staphylaea</i> Jousseaume, 1884	<i>Cypraea staphylaea</i> Linnaeus, 1758	8	7–39	0–150	Indo-Pacific
<i>Talostolida</i> Iredale, 1931	<i>Cypraea teres</i> Gmelin, 1791	8	12–49	0–100	Indo-Pacific and Eastern Pacific
<i>Talparia</i> Troschel, 1861	<i>Cypraea talpa</i> Linnaeus, 1758	2	23–106	0–35	Red Sea, Indo-Pacific
<i>Trona</i> Jousseaume, 1884	<i>Cypraea stercoraria</i> Linnaeus, 1758	1	26–97	0–1	West Africa
* <i>Umbilia</i> Jousseaume, 1884	<i>Cypraea umbilicata</i> Sowerby I, 1825 (= <i>hesitata</i> Iredale, 1916)	5	51–121	3–700	Southern Australia
* <i>Zoila</i> Jousseaume, 1884	<i>Cypraea scottii</i> Broderip, 1831 (= <i>friendii</i> Gray, 1831)	17	26–116	0–250	Southern Australia
<i>Zonaria</i> Jousseaume, 1884	<i>Cypraea zonaria</i> Gmelin, 1791	7	14–52	0–150	Mediterranean to West Africa
Average No. OTUs/genus		8.7 OTU/genus			
Range			6–190 mm	0–700 m	